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Art. VIII.—*The Ascent and Descent of Water in Trees.*

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(With Plate VII.).

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The question as to whether the aid of living wood tissue is necessary for the continuous conduction of water up lofty trees is still an unsettled one, being answered by some investigators in the affirmative, and by others in the negative. According to the theory put forward by Dixon and Joly, as well as by Askenasy, the ascent is wholly, or almost wholly, due to the suction exercised by the transpiring leaves upon the cohering columns of water suspended from them in the wood vessels; so that the water is drawn up from the roots in much the same way that a rope might be hauled up by hand. In a previous paper[1] it was pointed out that an explanation was required, not merely as to how the water was held suspended in the vessels, but also as to how the kinetic resistance to flow was overcome, and it was shown by calculation and experiment that in actively transpiring trees the total kinetic resistance to flow might be several times greater than the statical resistance due to the height of the tree. In other words, the suspended water columns in the vessels might at their highest points in the tallest trees, be under a tension equivalent not merely to a head of 300 feet of water, but to one of one or two thousand feet, or even more. Water columns are capable of standing such tensions, but only under conditions which are not presented in the wood vessels of trees—namely, the water columns must be entirely free from air or dissolved gases, they must be enclosed in rigid walls impermeable to water and to dissolved gases, and apparently, also, to judge from some of the experiments performed, the water must be as free as possible from suspended solid particles. Further, so far as I am aware, all the physical experiments which have been successful in demonstrating a high tensile strength for columns of water, have been carried out with stationary columns. It is quite an open question as to whether a column of water flowing with fair rapidity through a tube would exhibit the same tensile strength as a stationary one, particularly if its flow were interrupted by roughness and occasional transverse partitions, producing eddy currents or irregular flow instead of steady stream line flow. This question is, of course, one for physicists, but

1 Phil. Trans. Roy. Soc. London, B., vol. 198, 1905, p. 41

until it is answered it is not permissible to assume that the results obtained in glass tubes with stationary columns of water can be directly applied to the flowing columns of water, surrounded by the rough, water impregnated walls of the wood vessels, which are also readily permeable to air under pressure.

In a second paper, experiments were conducted on entire trees to determine whether any of the high tensions postulated in the water tension theory in the ascent of sap, could be detected in the wood of actively transpiring trees. The results obtained were in the negative, but, as pointed out by Dixon, the ordinary manometer experiments are unable to provide against the existence of air cavities in the wood tissue, so that the pressure exhibited by a manometer might be considerably less than that actually existing in the cavities of the wood vessels themselves. In any case this very fact makes it difficult to see how a high tension could be maintained for any length of time in a water column contained in a tube whose walls were saturated with water, and which bordered externally upon air spaces. The appearance of the minutest bubble of air in such a column of water would immediately cause its tension to be reduced to some fraction of an atmosphere. Actual observations, which have been confirmed by more than one observer, have shown that the wood vessels in the functioning wood of actively transpiring plants do actually contain bubbles of air, and hence cannot possibly transmit any tension exceeding an atmosphere.

In the same paper an account was given of an experiment with an entire tree, carried out on the same lines as those by Strasburger — namely, by cutting an entire tree at its base, and allowing first a poisonous and then a coloured solution to be drawn up the trunk of the tree. The experiments showed that there was a distinct tendency on the part of the sap to avoid the parts of the wood which had been killed by poison, and to flow in the older parts of the wood to which less poison had penetrated, but in which the flow is usually least active under normal conditions.

Apparently this pointed to the necessity of the existence of living wood cells to maintain the function of the wood vessels as conducting chambers, even for short lengths of time, and this would tend to show that the water tension theory only afforded a partial explanation of the ascent of water in tall trees. It was, however, obviously advisable to complete such observations by experiments carried out on the tallest trees available of 200 to 300 feet in height. The initial difficulty lay, however, firstly in the comparative inaccessibility of such trees for scientific experiments, and secondly in the difficulty and cost of carrying out the required manipulations, which would include very

1 Phil Trans. Roy. Soc. London, B, vol. 199, p. 341.

strong scaffolding and special apparatus for rapidly cutting the base of the tree and avoiding its exposure to air. Accordingly a simple preliminary experiment was tried upon a small tree of *Acacia mollissima* growing in the Herbarium grounds. The tree was four years old, 25 feet high, and had a circumference, 1½ feet above ground, of 26 inches. The spread of the tree was 14 feet, and the head was nearly cylindrical up to 6 feet from the top, the lowest branch being 5 feet from the ground. The base of the tree was surrounded by a cup made of canvas, and cemented until watertight. The cup had a capacity of 15 litres when filled up to a mark below the brim. In March, after filling the cup with water, a ring of bark and wood was cut away under the water near the base of the cup, by means of a sharp chisel, to a depth of 1½ inches all round the tree. The remaining core of wood was quite strong enough to support the entire tree, but was apparently inactive in the ascent of sap. (See Pl. VII.). Sufficient copper sulphate was then added to make a 5 per cent. solution, and after some 26 litres had been absorbed, which meant the addition of a large amount of water, the copper sulphate remaining was washed out and replaced by a solution of eosin. As can be seen from the data given beneath, the amount of water absorbed was considerable, but rapidly fell off after the first few hours.

Time.	Amount absorbed.	Conditions.
Wednesday, 13th		
10 a.m. - 11.30 a.m.	6 litres.	Bright sun
11.30 a.m. - 12.30 p.m	7 litres.	,,
12.30 p.m. - 1.30 p.m.	8½ litres.	,,
1.30 p.m. - 2.30 p.m.	5 litres.	,,
	Copper sulphate replaced by eosin.	
2.30 p.m. - 3.30 p.m.	4½ litres.	,,
3.30 p.m. - 4.30 p.m.	2½ litres.	,,
4.30 p.m. - 10.30 p.m.	9 litres. (1½ litres per hour)	
10.30 p.m. - 9.30 a.m.	11 litres. (1 litre per hour)	
Thursday, 14th		
9.30 a.m. - 10.30 a.m.	Fresh surfaces of wood cut	Overcast, clearing slightly to mid-day
10.30 a.m. - 11.30 a.m.	2 litres.	
11.30 a.m. - 12.30 p.m.	1½ litres.	
12.30 p.m. - 1.30 p.m.	2½ litres.	Cloudy
1.30 p.m. - 2.30 p.m.	1½ litres.	Sun and slight clouds
2.30 p.m. - 3.30 p.m.	1¾ litres.	Cloudy
3.30 p.m. - 4.30 p.m.	1 litre.	Slight sun
4.30 p.m. - 10.30 p.m.	5 litres (0.83 per hour)	
10.30 p.m. - 10.30 a.m.	5 litres (0.83 per hour)	
Friday, 15th.		
10.30 a.m. - 11.30 a.m.	¾ litre.	Bright sun
11.30 a.m. - 12.30 p.m.	1 litre.	,,

The following table from the Melbourne Observatory records gives the hygrometric conditions for the first day of the experiment.

March 13th, 1912.

Time	Dry Bulb	Wet Bulb.	Computed relative humidity. 100 = satuaration.	Evaporation at a free surface of water.
9 a.m.	62.5	55.2	63 per cent.	Amount of water evaporated
3 p.m.	65.3	56.0	54 ,, ,,	from 9 a.m. to 6 p.m.
6 p.m.	60.8	53.0	58 ,, ,,	0.086 inches.

With a spread of 14 feet diameter, the tree covered an area of ground of 142,588 square centimetres. With a rate of evaporation of 2.19 millimetres per 9 hours, this would give a total loss from a free surface of water of 31 litres, or 3.4 litres per hour. The estimated rate for the whole tree from branch observations made at 10 a.m., 1.30 p.m. and 4.30 p.m., represented an average total of 2.2 litres per hour during the same period. This is considerably less than the actual amount absorbed, and less than the amount that would have evaporated from a free surface of water covering the same area as the spread of the tree. Since the leaflets of the cut branches were, however, in all cases partially folded by the close of the experiment, it is possible that the estimated rate of transpiraton was somewhat less than actually occurred in the tree as a whole.

In all experiments in which eosin is used to indicate the ascent of water, the lateral diffusion of the dye makes it not altogether a perfectly safe guide as to the exact path of the water current. For this reason, copper sulphate was used as the poison to precede the eosin.

When copper sulphate is added to a strong solution of eosin, the greater part of the dye is precipitated, and hence it was thought that the ascending eosin would be fixed in the walls of the wood vessels by the copper sulphate impregnating them, and so largely or entirely prevented from lateral diffusion. This was actually the case. An examination of the wood showed the almost exclusive part played by the wood vessels in the ascent of sap. No indication could be seen of any connection of the medullary ray cells with the ascending stream, but as the copper sulphate had killed then before the eosin had entered the stem, this fact affords no evidence one way or another.

In addition, the presence of copper sulphate in the wood caused the eosin to be held back to such an extent as to make it useless as a measure of the movement of the sap. Thus when the tree was cut down at the end of the third day, eosin was only perceptible in the main trunk up to a height of 10 feet, and was entirely restricted to the outer layers of wood 1 to 1½ inches in depth at the base, and tapering to a depth of ¼ inch upwards.